Vol. 44 No. 10

BULLETIN

OF THE

TORREY BOTANICAL CLUB

OCTOBER, 1917

The structure and development of the plant association*

HENRY ALLAN GLEASON

Ecological literature has recently been enriched by the publication of an exceedingly important book (Clements, 3) on the structure and development of vegetation. Not only does the book present a thorough and detailed analysis of vegetation, based on the researches of the author, but it also reviews the theories and summarizes the facts from a vast array of the ecological literature. For all of its contents the working ecologist is grateful, although it is probable that some of the more radical ideas of the author may be accepted reluctantly and that others may be rejected completely.

Certain features of the monograph can scarcely be reconciled with his own by the writer of the present article. Since this paper does not pretend to be either a critique or a review, the writer will not attempt to discuss his objections in detail, but will merely mention what these features are. The chief one of them is the view of Clements, first expressed in 1905 (2), that the unit of vegetation (irrespective of its scope or of the term used to designate it) is an organism. Clements has also so enlarged the scope of the vegetational unit that it includes in his monograph not only a climax but also all the successional series leading to the climax. Thirdly, as a direct result of these two features, he has portrayed the phenomena of vegetation as exceedingly complex, requiring

[The BULLETIN for September (44: 411–462) was issued September 15, 1917.]

* Contribution No. 165 from the Botanical Department of the University of Michigan.

the introduction of several new terms into an already burdened terminology. Lastly, in developing his analytical scheme, several apparent exceptions have been excluded by definition.

Of the actual existence of definite units of vegetation there is no doubt. That these units have describable structure, that they appear, maintain themselves, and eventually disappear are observable facts. That to each of these phenomena a definite or an apparent cause may be assigned is evidenced by almost any piece of recent ecological literature. But the great mass of ecological facts revealed by observation and experiment may be classified in different ways, and from them general principles may be derived which differ widely in their meaning or even in their intelligibility.

There is offered in the following pages a series of general principles in explanation of the usual phenomena of vegetation, based chiefly on observations of the writer in his own field work. Some of these appear almost axiomatic in nature, and none can be supported here by a considerable volume of illustration because of lack of space. In general, they are synthetic rather than analytic in nature, and have been arranged to follow each other as nearly as possible in logical order.

I. THE INDIVIDUALISTIC CONCEPT OF ECOLOGY

1. The life of an individual plant is maintained and transmitted to its progeny by a complex of functions, operating by means of a complex of structures. Vegetation, in its broader aspects, is composed of a number of plant individuals. The development and maintenance of vegetation is therefore merely the resultant of the development and maintenance of the component individuals, and is favored, modified, retarded, or inhibited by all causes which influence the component plants.

According to this view, the phenomena of vegetation depend completely upon the phenomena of the individual. It is in sharp contrast with the view of Clements that the unit of vegetation is an organism, which exhibits a series of functions distinct from those of the individual and within which the individual plants play a part as subsidiary to the whole as that of a single tracheid within a tree.

It is true that various analogies may easily be drawn between a unit of vegetation and an organism, but these analogies are always more apparent than real, and never rise to the rank of homologies. For example, it is obvious that an association may appear on a new area, develop to maturity, and finally disappear, but these phenomena are in nowise comparable to the life history of an individual. A spore of *Rhizopus*, for example, given the proper environment, will grow to maturity and reproduce without the presence of any other living organism. The first pioneer species of an association, on the other hand, will merely reproduce themselves, and maturity of the association will never be reached unless its other species are also present in a neighboring area. Similar exceptions may be taken to all other analogies between the individual and the association, designed to demonstrate the organic entity of the latter.

2. Certain common phenomena of the plant individual, namely, migration of germules, germination, and growth, when performed *en masse* by numerous individuals, may produce visible effects which are worthy of special study and which demand a special terminology. Among these effects may be mentioned the structure of the plant association and of the subsidiary assemblages of plants within it, its space relation to neighboring associations, its development, and its ultimate disappearance.

II. THE ENVIRONMENT

3. The functions of the individual plant demand a proper environment for their operation. Any effective variation in the environment causes a variation in the performance of these functions, and many environmental changes produce also a variation in morphological structure. All these results may be investigated by experimental methods, and fall properly within the domain of morphology and physiology.

4. A fixed environment is probably never necessary to the life of any individual plant, and certainly never to any spermatophyte. Each individual is capable of existing under a variety of environmental conditions; as a simple example, the annual variation in temperature may be mentioned. Also, a fixed environment is not necessary to the life of all the individuals of one species.

The environment of a plant consists of the resultant of all the external factors acting upon it. Therefore individuals of the same species may occupy apparently different habitats and have different associates in different localities. This has been shown by numerous observers, and was definitely mentioned by Cowles in his classic paper of 1901 (4, p. 83). With one environmental factor near the optimum, others may apparently be near the minimum. Thus the tamarack, which in southern Michigan is confined to peat bogs, in Isle Royale occurs even in crevices in vertical rock cliffs.

Restriction of a certain type of environment to one portion of the range of a species may produce geographic variation in its structure, and possibly has a causative relation to the evolution of species. A well-known example is the Douglas fir, with its coastal and inland forms.

5. To state the matter with unnecessarily great refinement, it is probable that no two natural habitats have identical environments, and that no two species make identical environmental demands.

III. MIGRATION AND SELECTION

6. For continuous existence, every species has some form of reproduction. This invariably leads to the establishment of a new individual at some distance from the parent. Whether this distance be great or small, its passage by the germule constitutes migration.

The agents of migration, the devices of the germules which utilize the agent, the distance over which migration is probable, and other phases of the subject have all been frequently discussed in detail, and need no further mention here.

7. Migration may bring the germules into new types of environment, some of which may be effectively different from that of the parent plant. The extent of this effect depends upon the environmental diversity of the region and upon the mobility of the plant. For plants of little mobility, or for more mobile plants in a large area of essentially uniform environment, migration does not normally bring the germules into a new type of habitat. In general, also, there is no selective feature of migration by which the germule is regularly carried into areas of favorable environment.

8. Migration into an area comes only from the surrounding plant population within reach by the usual migration agents. The more mobile immigrants may therefore be drawn from a comparatively large area, while the immobile species must come from contiguous areas. The relation between migration and proximity has already been pointed out by Clements (1, p. 60). In general, for germules of equal mobility, it seems that the number entering any area varies inversely as the square of the distance of the source. This has been demonstrated for short migrations only. It is probable that beyond a distance which might be called the normal migration limit the migration of germules is only accidental. The actual population from which the immigrants of an area may be drawn is therefore a limited one occupying the surrounding region.

Within reasonable limits, depending upon the mobility of the species concerned, the immigrants of neighboring areas are similar, because they are derived from the same surrounding population. This is shown clearly in forest clearings, detached examples of which in the same region are immediately invaded and occupied by the same species. Conversely, the immigrants of widely separated regions are more or less dissimilar, even though their environments may be essentially alike.

9. Of all the immigrants into any area, only those may establish themselves which find in it environmental conditions within the limit of their own environmental demands. The actual mature immigrant population of an area is therefore controlled by two sets of factors: the nature of the surrounding population, determining the species of immigrants as explained in the preceding paragraph, and the environment, selecting the adapted species.

The difficulty of demonstrating the extent of migration and the species involved is at once apparent, since the migrating germules are almost always minute and difficult of detection among the native vegetation. Occasionally the interruption or modification of environmental selection permits the ecesis of unusually large numbers of individuals of a species which would otherwise have been excluded, and affords accordingly an idea of the great number of unsuccessful immigrating germules. Illustrations of this are commonly observed and only a single example need be cited. In the sand-dune region of Illinois, the single

passage of a wagon across the sand may bury to a proper depth for germination thousands of seeds of *Cassia Chamaecrista*, so that the course of the wagon is marked during the following summer by parallel lines of the plants. Obviously, migration has been general over the whole area, but environment has prevented ecesis except in this particular path.

10. The germules of the native species of any area are subject to the same environmental selection as those of the immigrants. But, since progeny generally closely resembles parent in structure and function, and accordingly in environmental demands, successive generations of native species and of successful immigrants may occupy an area continuously, unless the environment changes beyond the limits of the species, or the species vary into forms with new environmental demands.

11. In general, and for the average area, opportunities for immigration have existed for so long a time that a complete selection from the surrounding population has been made. Such areas, therefore, show no changes in their population from year to year until the environment or the surrounding population becomes changed. The effects of such changes are discussed in part VII of this paper. When they occur, the resulting change in the component species is at once evident, since migration has continually supplied the area with the germules of hitherto unsuccessful species.

IV. THE ASSOCIATION, ITS SIZE AND BOUNDARIES

12. Whether the population is immigrant or native, it is always subject to the selective action of the environment. In the same limited region, that is, with the same surrounding population, areas of similar environment, whether continuous or detached, are therefore occupied by similar assemblages of species. Such an assemblage is called a plant association.

The term to be applied to such an assemblage, whether association, formation, or something else, and the method of characterizing and distinguishing one from another, are still matters of discussion. The writer believes that the term association is the best designation, and that this term has been applied by a majority of ecological authors to just such assemblages as those defined above.

13. One of the most important features of the environment is the control or modification of the original physical factors by the plant population itself. This action of plant life has been discussed repeatedly and requires no further argument here. As simple examples only, there may be mentioned the reduction of the light for the smaller plants by the crowns of the larger ones, and the modification of soil by the addition of organic substance. This control is in general directly proportional to the density of the plant population. In areas whose physical environment is generally genial and favorable to the development of numerous individuals, the resulting dense vegetation controls to a large degree the original physical factors, and this environmental control is of greater importance than those in the selection of the plant population.

It is at once obvious that, as a result of environmental control, the associated species of even the most limited area do not always enjoy the same environment. Thus the relations of a mature forest tree to light, wind, and soil are very different from those of the shallow-rooted, shade-loving, secondary species beneath it.

The physical factors of the environment generally vary gradually in space. Exceptions to this condition may easily be found in the soil factor, where sharp variations frequently occur, such as the contact of sand with clay at the foot of an advancing dune, or less obviously in the water factor, as on the rocky shore of a lake. Such gradual and progressive variation of environment would normally lead to equally gradual and progressive changes in the vegetation and to the establishment of broad transition zones between adjacent associations, in which the species of both mingle. In most regions of extreme physical environment, occupied by sparse vegetation exerting little environmental control, this condition holds, and the transition from one association to another is just as gradual as the change of environment.*

In regions of genial environment and dense vegetation, on the other hand, the nature of the environmental control of two ad-

* This condition has in fact led some students to complain that it was difficult or impossible to distinguish associations in the vegetation of the western states. This would be a sad state of affairs if all vegetation were composed of definite organic entities, but is quite to be expected when vegetation depends upon environmental selection of favored individuals.

jacent associations may be, and usually is, very different. Species of one association are then excluded from the margin of the other by environmental control, when the nature of the physical factors alone would permit their immigration. The adjacent associations therefore meet with a narrow transition zone, even though the variation in physical environment from one to the other is gradual.

In such regions of great environmental control, the boundary between two associations seldom marks the extreme location of suitable physical environment for either, but rather some intermediate position (see also paragraph 25). The removal of either association at one portion of the boundary results accordingly in an immediate extension of the other. This may be seen around many small lakes in Michigan, where a zone of sedge is followed in deeper water by a zone of water lilies. Destruction of the sedge zone in the shallower water is followed by the extension of the lily zone almost or quite to the shore line. The normal landward margin of the water lily association is therefore determined not by depth of water alone, which represents the chief physical environmental variant, but also by the environmental control of the sedge association.

14. Instances may be cited where the sole environmental difference between two adjacent associations lies in the environmental control. This is notably the case with some types of prairie and upland forest in the Middle West. The differentiation of two distinct associations in the same environment is then to be explained chiefly, if not entirely, by developmental conditions, as discussed below under Succession.

15. The line which marks the boundary of the distribution of a species is located at right angles to the direction of the effective environmental variant. Consequently the boundary of the whole assemblage of species constituting the plant association has the same position, whether the variant be purely physical or biotic. Since physical factors generally vary irregularly from place to place, the boundary and shape of an association are also usually irregular.

Symmetry or regularity in the variation of an important environmental factor may however occur. The most conspicuous example is the variation in depth of water or in amount of soil

water near the shore of a pond. In such cases, regularity in the environment produces a similar regularity in the arrangement of the associations. When this is conspicuous enough to attract the attention of the observer it is termed zonation.

Zonation of associations is the exception rather than the rule and has no more significance than the usual irregular arrangement. Between the two types there are naturally intermediate stages. Also, irregularity in other conditions affecting the differentiation of associations may operate to disturb their zonation. This has been frequently described or figured (see Harshberger, **8**, p. 382, 383) by investigators, generally without a statement of the cause.

16. The area occupied by an association may be large or small, depending on the size of the area available without effective environmental variation. Zoned associations about a pond frequently have dimensions conveniently expressed by meters (see Gates, **5**, p. 329), while some forest associations are better measured by the kilometer. The smaller associations are usually composed of fewer species, and are generally of shorter duration than the larger ones. They are the product of the same kind of causes, however, and are no less important in the ecological study of vegetation.

Since associations often tend to extend their area at the expense of others, as discussed below (part VII), the observed size of an association is correlated with its developmental history, and must always be considered from that standpoint.

V. THE STRUCTURE OF THE ASSOCIATION

17. The general tendency of the population of an association to migration tends to produce uniform distribution of each species within it, and consequently uniformity of the association as a whole. This uniformity is one of the most characteristic visible features of the association, and has by some been taken as the basis for a definition of it (**6**, p. 36). It is easily demonstrable in the small associations and in large ones becomes very impressive. The chief value of the quadrat method of expressing the structure of vegetation depends upon this feature, since a small area can be chosen for intensive study which exhibits faithfully the average structure of the whole association.

Since migration requires time, uniformity of any species is an expression (to be considered in comparison with its mobility) of the length of time it has been in the association, and general uniformity of an association is regularly correlated with its age. As illustration, the uniformity of a forest may be compared with the lack of uniformity in the clearing association which develops soon after lumbering.

18. Excessive seed production is almost universal among plants, and leads to a great competition for the environment. The number of individuals of a species is therefore an expression of the degree of its adaptation to the environment. In the rapid development of an association over a considerable area of ground, as a forest clearing, the most mobile species is naturally represented at first by the greatest number of individuals, irrespective of its adaptation, but as soon as the ground is occupied competition restricts it to its proper proportion.

19. Within an association, minor variations in environment may affect certain susceptible species and not others, and as a result produce minor deviations from the usual uniformity. For example, in an area of woodland in central Illinois, of otherwise uniform structure, a shallow valley is occupied every spring by large numbers of *Floerkea proserpinacoides*. In this case the controlling feature seems to be the greater amount of water in the surface soil during the spring months. For other plants at the same season, and for all plants during the summer and autumn, this feature seems to be without effect.

Recent introduction or slow migration of a species may also produce colonies which interrupt the general uniformity. An instance of the former case has been described (**7**, p. 520, 521) in the migration of introduced species into the aspen association of northern Michigan. Colonies of the second type are generally caused by the vegetative reproduction of the species, and the resulting compact groups of individuals have been termed families by Clements (**2**, p. 203).

Among the larger, longer-lived, dominant species, accidents of immigration, such as proximity or a good seed year for one species, may cause the development of minor groups within the association, characterized by a few or only one of its usual dominants.

To such groups Clements has applied the term consocies. Since the individuals of these groups occupy the ground closely from the beginning, they may exclude completely the development of the other dominants of the association until they finally die of old age, when contemporaneous conditions will again decide what species occupy their places. Since dominant species of the same vegetative form have in general similar powers of environmental control, the secondary species beneath a consocies are essentially similar to those elsewhere in the association. For the same reason, the development of minor structural units among the secondaries has little or no relation to the composition of the dominants.

Only rigid experiment and careful observation will refer lack of uniformity accurately to one or another of the causes suggested here.

VI. SCOPE OF THE ASSOCIATION

20. Because of differences in the surrounding plant population, from which the inhabitants of an area are drawn; because of accidents of migration and the time available for it; and because of environmental differences, no two areas need have identical populations, measured by component species and the relative number of individuals of each. This is demonstrable even for areas within a restricted region, and is especially obvious in a comparison of two areas widely separated. For example, no two areas of the beech-maple association near the Biological Station of the University of Michigan show the same vegetational composition, and much greater differences are found when those are compared with the beech-maple forests of southern Michigan, 500 km. away. Still the beech-maple forest has always been interpreted as a single association of wide extent.

Whether any two areas, either contiguous or separated, represent the same plant association, detached examples of the same one, consocies, or different associations, and how much variation of structure may be allowed within an association without affecting its identity, are both purely academic questions, since the association represents merely the coincidence of certain plant individuals and is not an organic entity of itself. While the similarity of vegetation in two detached areas may be striking, it is only an

expression of similar environmental conditions and similar surrounding plant population. If they are for convenience described under the same name, this treatment is in no wise comparable to the inclusion of several plant individuals in one species.

VII. SUCCESSION

21. Any change in the association, from any cause whatever, either in the component species or in their relative numbers of individuals, marks a step in the development of vegetation. If this change eventually becomes so great as to involve the replacement of the original association by a different one, the process is known as succession.

Under this definition, the inclusion of any developmental phenomenon under the term succession depends entirely upon the concept of the association held by the investigator. According to general custom, the association is defined broadly enough to permit considerable variation in its structure. Any structural changes within this limit may be referred to minor or periodic environmental changes or to the immigration of relatively unimportant species, and are not considered as succession.

Just as there is a transition zone in space between two contiguous associations, where the species of both mingle, so is there also a transition period between the disappearance of the original association and the complete establishment of the new one, during which relic species of the former and pioneer species of the latter exist side by side. Causes similar to those which decide the width of the transition zone also determine the duration of the transition period. This will be relatively long between associations of similar or slight environmental control and in cases of gradual environmental change, and relatively short between associations of different or great environmental control and in cases of rapid environmental change.

22. Arrival within migration distance of a new population with similar environmental demands (or overlapping ranges of demands) results in fresh immigration and a consequent change in the population of an association. This immigration is limited to those members of the new population which are adjusted to the environmental control of the original association. If these im-

migrants are adapted to the new control in a manner similar to the original secondary species, they behave as secondaries also, and henceforth constitute what has been called the derived element of the population. A noteworthy illustration is found in the prairies of the Middle West, which invariably contain a number of typically forest species, such as *Geranium maculatum* and *Phlox pilosa*.

But if the immigrants are adapted to the original control as seedlings and exert a different sort of control at maturity, they may themselves become dominant. Their establishment then results in the selection of new secondary species, as already discussed (paragraph 9), and the completion of the succession. This process is illustrated in the reëstablishment of forests on the cut-over lands of northern Michigan, where the seedling hardwoods appear as secondary species beneath the dominant aspens. Approaching maturity, they control the light and soil factors of the environment to the ultimate exclusion of the aspens.

Successions of this sort, initiated without environmental change, whether partial or complete, operate over the entire area involved, but will normally be most immediately effective near the margin, because of proximity to the source of immigration.

23. The common cause of succession is an effective change in the environment. This may consist of a change in the physical factors due to inorganic agents, to reaction of the plant upon its environment, due to the cumulative effect of environmental control, or to a combination of the two.

An effective change of environment beyond the range of demand of any individual (or species) causes its death (or extinction). Such effective changes are usually slow in development. In average cases, extinction of a species in an association means death of established plants merely by old age and an increasing death rate by competition among the seedlings. Violent changes, as in the rapid erosion of river banks or the movement of shifting dunes, may actually kill mature plants, but these are comparatively rare. Death of any plant removes its environmental control and may consequently lead to the death of other plants which have depended upon it.

Simultaneously with the death of the old population, the changed environment selects a different new population from the immigrants, and a new association appears.

In regions of sparse vegetation, succession is usually due to changes in the physical environment. In regions of dense population, the same causes are still active, but reaction is usually more rapid and more effective. Physical changes may be retarded by control or reaction, as in the reduction of run-off and erosion by a forest cover, or hastened, as in the weathering of a rock cliff. The effect of slow physical change may also be neutralized for a time by the stability and completeness of the more important environmental control. Thus certain sand hills in Illinois are continually losing a little sand by wind action, but this is sufficiently controlled by the bunch-grass association and no succession occurs.

In successions due to either sort of environmental change, the most mobile species of the invading association normally arrive first and constitute the pioneers. The first species to disappear are those most intimately dependent upon proper control or most narrowly adjusted to the environment. In the climate of the Middle West, these are usually the secondary species. Both for the reason just mentioned and because of their usually longer life, the relic species are more frequently selected from the original dominants.

24. A continued and progressive change in one factor or in a group of factors results in a series of successive associations, which follow each other on the same area of ground. Familiar examples are the decrease in water in the filling of a pond, and the simultaneous increase in humus and decrease in light in the development of a forest.

In any region, similar environmental processes are usually operative in many stations, and since the associations of such successional series must be selected from the same surrounding population, the successive stages of the series in all stations are essentially similar also. Uniformity of successional series may therefore be expected only within regions of similar population and upon areas of similar environmental change. Thus the stages accompanying the filling of a pond by peat formation are not the same in northern and southern Michigan, notwithstanding the similarity in process, because of the difference in surrounding population; and in either region the filling of ponds by peat and by wind-blown sand is accompanied by different successional series because of the difference in process.

The same environmental processes may not continue in operation long enough to effect the completion of the series. Thus a lagoon in northern Michigan, isolated from a lake by a sand-bar, begins its process of extinction by filling with wind-blown sand. For some time this process of topographic filling is more important than the deposition of organic material, and a series of associations representing a sandy marsh is developed. Later, the establish- of shore thickets on the sand-bar between the lagoon and the lake excludes the sand. Further filling of the pond then depends upon organic deposits, and with the accumulation of peat the associations of a peat bog gradually replace those of the sandy marsh.

Another cause of variation in successional series is found in the accidents of immigration, which may lead to the establishment of several consocies even in the same environment. With all these opportunities for deviation from a simple series, it is easy to understand why carefully constructed successional diagrams are sometimes so complex (Gates, **5**, *pl. 39;* Sernander, **9**).

25. The duration of an association is merely an expression of the rate of environmental change, irrespective of its cause. Associations of dense vegetation normally hold their place far beyond the period of optimum environment, because of environmental control, competition, and difficulties of immigration, finally yielding only when the environment is approaching the optimum of the succeeding association. This condition was clearly recognized by Cowles (**4**, p. 79), who termed it "a lagging of effects behind their cumulative causes."

Stability of an association, whether for a long period or a short one, is due to cessation of environmental change, or to the greater effect of environmental control.

26. The location of the initiation of topographic changes is theoretically independent of position within the association. Practically, however, it is almost always at the margin and of such a nature as to produce the environment of the neighboring association. Succession is accordingly usually between adjacent associations. Progressive changes of environment due to physical causes are frequently unilateral, an environmental type appearing on one side of an area, advancing across it, and disappearing on

the other. The accompanying associations therefore lose ground on one side as they gain it on the other, and when the rate of gain and loss are about equal the association as a whole may seem to change its position. Such progressive changes are usually correlated with a regular or symmetrical distribution of environment, so that zonation becomes an epitome of succession. Then the transition zone indicates the location of succession and endures in the same position merely for the transition period.

Succession by reaction begins wherever and whenever effective reaction is completed. This is normally in the oldest part of the association, the location of which may be either central or lateral, depending upon the circumstances of its origin. In either case the result is the same. Proximity, governing the opportunity of immigration, limits the pioneer species in central succession to the most mobile forms. Thus, in the central succession of the black oak association by the mixed forest in Illinois, the most conspicuous pioneer species is the permobile avevectent *Psedera quinquefolia* (**6**, p. 136).

The reaction of an association may also extend beyond its actual margin and produce an effect upon the margin of the contiguous association. If this weakens the environmental control in the latter, an advance of the former association takes place. This is the case in the advance of upland forest on the prairies of the Middle West. Since the sod-forming grasses grow less vigorously in the partial shade of the forest margin, the sod there is less dense and seedlings of forest species can establish themselves. The average rate of advance under these conditions was estimated by the late Professor Burrill at fourteen feet per year.

27. Some associations make no unfavorable reaction on their environment, live under conditions not subject to effective change by the usual topographic agencies of the region, and are not near a different type of vegetation better adapted to the same environment. In the absence of all causes of succession, such associations occupy the area permanently and are called climax. Theoretically, all associations of a region tend to culminate in the establishment of a climax. Many associations, however, occupy their ground so tenaciously that there is little or no observable evidence that they are ever replaced by the association ordinarily considered

to be the climax of that region. Such is the case with the oak-hickory forests of the gravel hills of southern Michigan. Even if the cumulative effect of exceedingly slow physiographic and biotic processes should accomplish this result and lead to their succession by the beech-maple forests, the same fate is not necessarily in store for similar forests of western Iowa, where neither beech nor maple occur. It is always possible, also, that the future may bring an effective change of environment, no indication of which is at present visible. A slight change of rainfall, for example, might lead to the extension of the pine forests of the Rocky Mountains over the high plains of eastern Colorado. The use of the term climax is accordingly largely a matter of convenience, and it will be applied broadly or narrowly, depending on the viewpoint of the ecologist.

Since physiographic processes tend toward stability, successional series tend also toward the establishment of associations of greater duration and the ultimate appearance of a climax. In some cases, as the succession of forest by prairie, this involves a process which is not usual for our climate, or not commonly observed, and which has been termed regressive or retrogressive. In other cases also, an actual reversal of the ordinary direction of succession may be seen, as in the establishment of a pond upon a sand dune (**6**, p. 111–116). Clements denies the existence of reversed successions, and attempts to exclude described cases by definition (**3**, p. 145, 146). Measured by the behavior of and effects upon individual plants, however, the processes are precisely the same as in the usual types of succession: a change of environment, the gradual death of the original flora, and the gradual entrance of the new, with the simultaneous revision of environmental control.

28. Great climatic changes in a region, when they occur, are of course productive of proportionately great changes in the vegetation, involving ultimately perhaps the complete replacement of all the original associations by new ones. Without the arrival of a new flora in the region, the change in the original vegetation as the result of climatic change can consist only of the extinction of unadapted species, their replacement wholly or in part by species of recent evolution, and of readjustments in the

plant associations concerned. Such events are so slow that they have never been described from observation, and it is extremely doubtful if the term succession would be applied to them if they were visible.

The actual effect of climatic changes as seen consists of the arrival in the region of a new flora, the establishment of successions between its associations and the original ones, and the gradual replacement of the latter. It is possible that temperature changes have never taken place in the past more rapidly than they are proceeding at present, and that is at a rate too slow to be measured. The effect of such changes, however, are seen in the northward advance of the hardwood forests at the expense of the conifers. As has been repeatedly shown by various authors, the successions involved here are invariably referable to one or another of the causes already discussed in these pages, and no direct effect of a temperature change is visible at all, so far as the structure or succession of associations is concerned.

Great climatic changes, therefore, proceed at a much slower rate than the normal observable causes of succession. Those great successional movements which have marked the development of the flora of the continent through all the climatic and geologic vicissitudes of the epochs, and whose results are now exhibited by the geographical distribution of the flora, are merely the mass effects of small successions, coupled with the evolutionary phenomena of extinction and appearance of species.

SUMMARY

1. All phenomena of vegetation, *i. e.*, of numbers of individuals, depend upon the phenomena of the individual plant.

2. The plant population of any area is determined by environmental selection of immigrants from the surrounding population.

3. Because of similarity of environmental selection and of available sources of immigration, areas of uniform vegetation are developed, known as plant associations.

4. Effective changes in the environment or in the surrounding population may lead to significant changes in the vegetation of an area. If these changes involve the establishment upon it of a new association, the phenomenon is known as succession.

UNIVERSITY OF MICHIGAN,
ANN ARBOR, MICHIGAN

LITERATURE CITED

1. **Clements, F. E.** The development and structure of vegetation. Bot. Surv. Nebraska **7.** 1904.
2. **Clements, F. E.** Research methods in ecology. Lincoln, Nebraska. 1905.
3. **Clements, F. E.** Plant succession. Carnegie Inst. of Washington, Publ. 242. 1916.
4. **Cowles, H. C.** The physiographic ecology of Chicago and vicinity. Bot. Gaz. **31:** 73–108, 145–182. *f. 1–35.* 1901.
5. **Gates, F. C.** The vegetation of the beach area in northeastern Illinois and southeastern Wisconsin. Bull. Illinois State Lab. Nat. Hist. **9:** 255–372. 1912.
6. **Gleason, H. A.** The vegetation of the inland sand deposits of Illinois. Bull. Illinois State Lab. Nat. Hist. **9:** 23–174. *pl. 1–20.* 1910.
7. **Gleason, H. A., & McFarland, F. T.** The introduced vegetation in the vicinity of Douglas Lake, Michigan. Bull. Torrey Club **41:** 511–521. 1914.
8. **Harshberger, J. W.** The vegetation of the salt marshes and of the salt and fresh water ponds of northern coastal New Jersey. Proc. Acad. Nat. Sci. Philadelphia 1909: 373–400. *f. 1–6.* 1909.
9. **Sernander, R.** De scanodaniska torfmossarnas stratigrafi. Geol. För. Stockholm Förhandl. **31:** 423–448. *f. 1.* 1909. Review in Bot. Centr. **114:** 189, 190. 1910.